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TIME OF SUPPLEMENTAL FEEDING ALTERS THE EFFECTS OF COCAINE ON LEVER PRESSING OF RATS

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The present experiment assessed the effects of cocaine on the lever pressing of 4 rats maintained during 15-min sessions by a fixed-ratio 50 schedule of food reinforcement. Across phases, supplemental food was provided either immediately or 2 hr after sessions. Two rats began the experiment in the delayed-feeding condition, and 2 began the experiment in the immediate-feeding condition. Rates of lever pressing of 2 rats sometimes decreased to low levels near the ends of sessions when supplemental feeding was provided immediately, but were consistently high throughout sessions when supplemental feeding was delayed. Cocaine (1.0 to 17.0 or 30.0 mg/kg) was administered intraperitoneally 15 min prior to test sessions. In most cases, cocaine suppressed response rates at lower doses under immediate-feeding conditions. Decreases in overall response rates were correlated with dose-dependent increases in the time rats spent not responding. It is suggested that delaying the time of postsession feeding increased response strength, as indicated by greater resistance to the rate-suppressive effects of cocaine.

Key words: cocaine, fixed-ratio schedule, response strength, supplemental feeding, rats

The psychomotor stimulants cocaine and *d*-amphetamine usually decrease rates of operant behavior maintained by fixed-ratio (FR) schedules of reinforcement in a dose-dependent fashion (Gonzalez & Goldberg, 1977; MacPhail & Seiden, 1975; McMillan, 1969; Smith, 1964; Woolverton, Kandel, & Schuster, 1978a, 1978b). Rate decreases can be altered by several conditions. For example, cocaine has been shown to suppress pigeons' rates of pecking maintained by large ratio values more readily than rates maintained by low ratio values (Hoffman, Branch, & Sizemore, 1987). Also, rates of food-, water-, and milk-reinforced behavior are decreased less under more severe conditions of food or water deprivation (Gollub & Mann, 1969; MacPhail & Gollub, 1974; MacPhail & Seiden, 1975; Samson, 1986). Schaal and Branch (1992), for example, showed that cocaine suppressed rates of pecking in pigeons maintained by an FR 30 schedule of food presentation more readily when they were relatively satiated than when they were more food deprived. This result was replicated in a study that also showed that food deprivation enhanced the rate-increasing effect of cocaine under fixed-interval (FI) schedules (Schaal, Miller, & Odum, 1995). The rate-suppressive effects of methadone also have been shown to depend on levels of food deprivation (Kelly & Thompson, 1988) and on reinforcement rates experienced both prior to (Egli, Schaal, Thompson, & Cleary, 1992) and during (Egli & Thompson, 1989) sessions in which drugs are tested.

The variety of circumstances under which effects such as these have been observed suggests that the disruption of operant behavior by drugs frequently depends on the baseline strength of that behavior. Response strength may be conceived of as the tendency for behavior to persist in the presence of circumstances that suppress it (Nevin, 1974). These circumstances include motivational variables, extinction, punishment, and, under some conditions, drug administration. This experiment was designed to test whether the time to postsession feeding, another variable that often alters the persistence of behavior, also alters the resistance of the behavior to the rate-suppressive effects of cocaine.

In operant conditioning experiments in which food is the reinforcer, food deprivation is usually arranged by lowering body weights. Food in addition to that consumed within ses-

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sions (i.e., supplemental food) is provided following sessions to maintain weights within a given range. Several experiments have shown that the manner in which supplemental food is provided outside the experimental setting can influence rates of responding during experimental sessions (Bacotti, 1976; Collier, Johnson, & Morgan, 1992; Elsmore, 1979; Hursh, 1978; Lucas, Gawley, & Timberlake, 1988; Timberlake, 1984; Timberlake, Gawley, & Lucas, 1987; Timberlake & Peden, 1987; but see McSweeney, Hatfield, & Allen, 1990). For example, Collier et al. exposed rats to two FR schedule values (10 and 40) and three pellet sizes (20, 45, and 97 mg). When rats lever pressed for all of their food during whole-day sessions, response rates were highest during the FR 40 schedule of 20-mg pellet delivery. When supplemental feeding was provided after 30-min sessions, rates of responding decreased as pellet size increased under the FR 10 schedule, and were not affected by pellet size under the FR 40 schedule. Thus, rates of responding during sessions increased or decreased in a manner that ensured a relatively constant daily amount of food. In another study with rats (Timberlake, 1984), responding on a progressive-ratio schedule of food reinforcement was lower when response-independent food was provided within 16 min of the start of the session. Delaying response-independent food for longer periods of time did not alter rates of responding. Experiments such as these suggest that longer delays to supplemental feeding, or the absence of supplemental food, produce higher rates of responding relative to conditions in which supplemental feeding is provided immediately after sessions, and thus may increase the strength of operant behavior maintained by food.

The purpose of the present study was to determine whether delays to supplemental feeding would alter the behavioral effects of cocaine. With the exception of the investigation of the effects of food deprivation on drug self-administration (see review by Carroll & Meisch, 1984), the behavioral effects of drugs have not been examined under different conditions of supplemental feeding. In this study the effects of cocaine on food-reinforced behavior were tested when rats were fed either immediately following sessions or 2 hr later. If, as suggested by the behavioral research, immediate versus delayed supplemental feeding affects the strength of behavior during the session, then cocaine should suppress rates more readily when rats are fed immediately after sessions.

METHOD

Subjects

Four male Sprague-Dawley rats were approximately 270 days old at the start of the experiment. They had responded under several FR schedules (FR 5, 10, 30, and 50) of food delivery and several delays to supplemental feeding prior to this study, beginning when they were 120 days old. When not in experimental sessions, they were individually housed with free access to water under a 12:12 hr light/dark cycle. Sessions were conducted approximately 2 hr after the dark part of the cycle started at 7:00 a.m.

Apparatus

Four custom-built chambers were used. The interiors of the chambers were 28.5 cm long, 25 cm wide, and 20 cm high. The side walls and ceilings were constructed of Plexiglas, the end walls were aluminum, and the grid floor was constructed of stainless steel rods. Two aluminum levers, spaced 13.5 cm apart and 5 cm from the grid floor, required 0.25 N to operate. Only the left lever was used. Lamps (28 V) covered with white plastic caps were mounted 5 cm above each lever. A houselight mounted above the chamber provided general illumination. Food pellets could be delivered into a circular aperture measuring 3.5 cm in diameter and centered between the levers. Each operant chamber was housed in a sound- and light-attenuating enclosure. White noise and noise from a ventilation fan masked extraneous sounds. Contingencies were programmed and data were collected using microcomputers located in an adjacent room.

Procedure

Sessions were conducted 7 days per week at approximately the same time each day. Lever pressing was maintained under an FR 50 schedule of food-pellet (45-mg Noyes) delivery during 15-min sessions. Initially, 2 rats (L6 and L7) received supplemental food imme-

diately following sessions, and 2 rats (L5 and L8) were fed 2 hr after the session. A specific regimen of feeding, weighing, and handling the rats was followed throughout the study. Rats were always weighed prior to sessions. At the end of the session, rats were removed immediately from the chambers and returned to their home cages in less than 5 min. If rats were in the immediate-feeding condition, food was placed in the home cages while the session was in progress. During the delayed-feeding condition, food was provided 2 hr after the session. Supplemental feeding consisted of 1 hr of access to laboratory rat chow according to the method proposed by Hurwitz and Davis (1983), which allows the weights of rats to increase slowly during the study while a level of food deprivation sufficient to maintain stable rates of pressing is maintained. In both feeding conditions, food that had not been eaten after 1 hr was removed from the cages.

Stable responding was determined by examining response rates in successive 3-min segments of sessions. Only the mean rates of responding in the first three segments were used to determine stability because responding sometimes decreased in the final two segments when supplemental feeding occurred immediately. Responding was considered to be stable if the difference between the mean rates in the first three of the most recent six sessions and the last three of the most recent six sessions was less than 5% of the overall six-session mean (Schoenfeld, Cumming, & Hearst, 1956) and if there was no indication of an increasing or decreasing trend across the last six sessions. Conditions were not changed and cocaine was not tested until these criteria were met. Following the initial tests of cocaine, rats were switched to the feeding condition they had not yet experienced and response rates were allowed to stablize prior to a second series of dose–effect tests. To determine whether the order of exposure to the feeding conditions altered the effects of cocaine, the rats were then returned to their original feeding conditions and a single ascending series of dose–effect tests was conducted. Table 1 presents the order of conditions, the number of sessions that preceded the initiation of cocaine dose–effect tests, and the body weights obtained for each rat prior to the first drug test session of each feeding condition.

Table 1

Order of conditions, number of sessions preceeding drug tests, and body weights obtained for each rat prior to the first drug test of each feeding condition.

Condition	Rat	Feeding	Sessions	Weight (g)
1	L5	Delayed	24	386
	L8	Delayed	24	420
	L6	Immediate	22	388
	L7	Immediate	23	369
2	L5	Immediate	9	428
	L8	Immediate	8	497
	L6	Delayed	13	421
	L7	Delayed	8	389
Reversal	L5	Delayed	9	442
	L8	Delayed	8	508
	L6	Immediate	13	432
	L7	Immediate	8	402

Cocaine hydrochloride (National Institute on Drug Abuse) was dissolved in 0.9% saline to be injected intraperitoneally in a volume of 1.0 ml/kg. Following injections, rats were placed in the operant chambers, and sessions began 15 min later. In the first two phases, doses were tested in an ascending (saline, 1.0, 3.0, 5.6, 10.0, and 17.0 mg/kg) then a descending order. In the last phase, doses were tested only in ascending order. A third test of 10.0 mg/kg was conducted for Rat L6 during its second condition (with delayed supplemental feeding). For Rats L6 and L7, 30.0 mg/kg was administered under the delayed-feeding condition because 17.0 mg/kg produced no change in response rates. At least four sessions in which no drug was given separated drug tests.

Overall response rates and rates in successive 3-min segments of the sessions were computed. In addition, the time of each lever press and reinforcer was collected and used to isolate time spent pressing from time spent not pressing to assess the manner in which cocaine reduced overall response rates. Finally, a statistic proposed by Nevin, Smith, and Roberts (1987) to represent the overall effects of a behaviorally disruptive event (in this case, administration of cocaine) on behavior maintained at different strengths (in this case, by altering the delay to supplemental feeding) was employed. The formula for computing the statistic, f, is

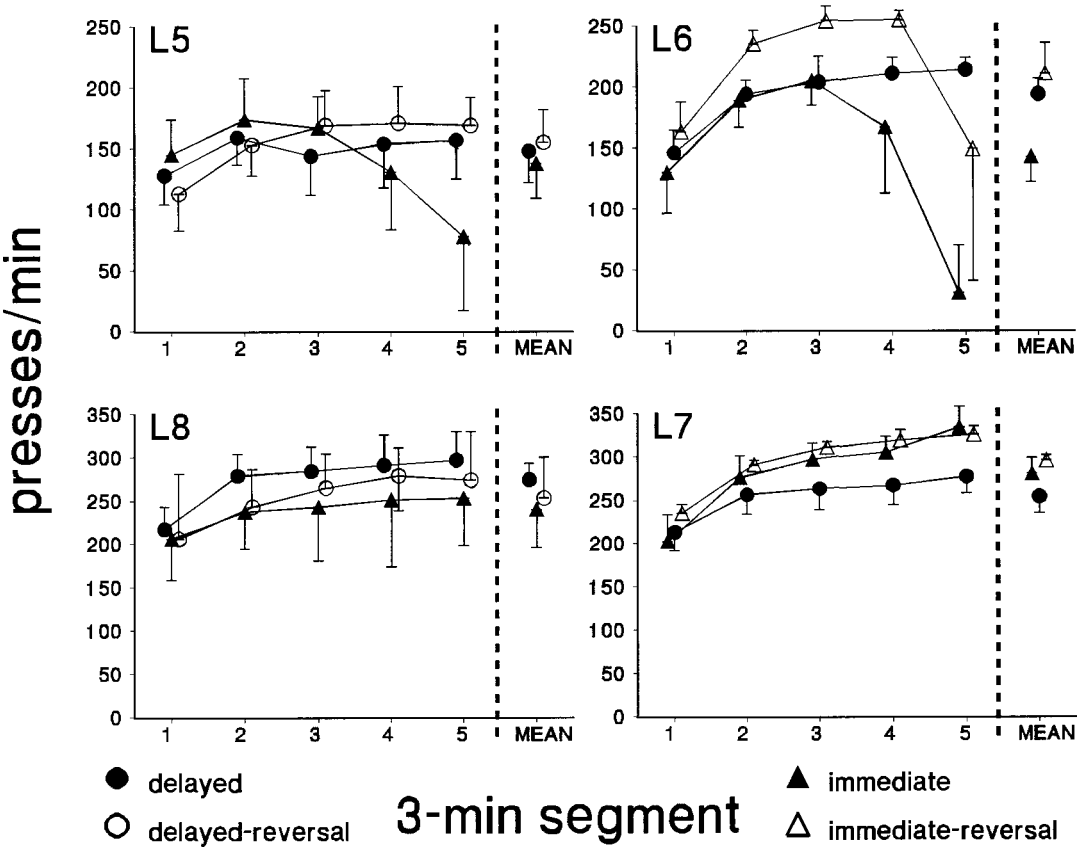

Fig. 1. Mean baseline response rates under an FR 50 schedule of reinforcement in each successive 3-min segment of the sessions during the last six sessions prior to cocaine tests in each of the supplemental feeding conditions. The filled circles represent delayed-feeding conditions, filled triangles represent immediate-feeding conditions, open circles represent reversal to delayed-feeding conditions, and open triangles represent reversal to immediate-feeding conditions. Error bars represent ±1 *SD*.

$$\bar{p} = \frac{\sum x_i p_i}{\sum x_i},$$

where x_i is the ith drug dose and p_i is the proportion of baseline responding produced by that dose. The statistic quantifies and summarizes performance over a range of values of a disruptive variable. Because lower values of the disrupter are less likely to have an effect, the statistic gives greater weight to higher values. The statistic $\bar{p}$, then, is a weighted mean of the proportional reductions in response rates produced by cocaine.

RESULTS

Figure 1 presents baseline response rates during successive 3-min segments of 15-min sessions that preceded sessions in which cocaine was tested. Overall response rates (plotted above "MEAN" in Figure 1) were not consistently or substantially different as a function of condition, but response rates differed across the session. During the delayed-feeding condition, response rates increased slightly from the first to the second or third 3-min period, and then were high (approximately 160 to 320 presses per minute) and steady for the rest of the session. During the immediate-feeding condition, the same pattern occurred except that rates of Rats L5 and L6 sometimes decreased near the end of the session, which resulted in mean curves that were an inverted-U shape. Under reversal conditions, the patterns of changes in rate across the session were similar to those obtained during the initial exposure to the first feeding condition.

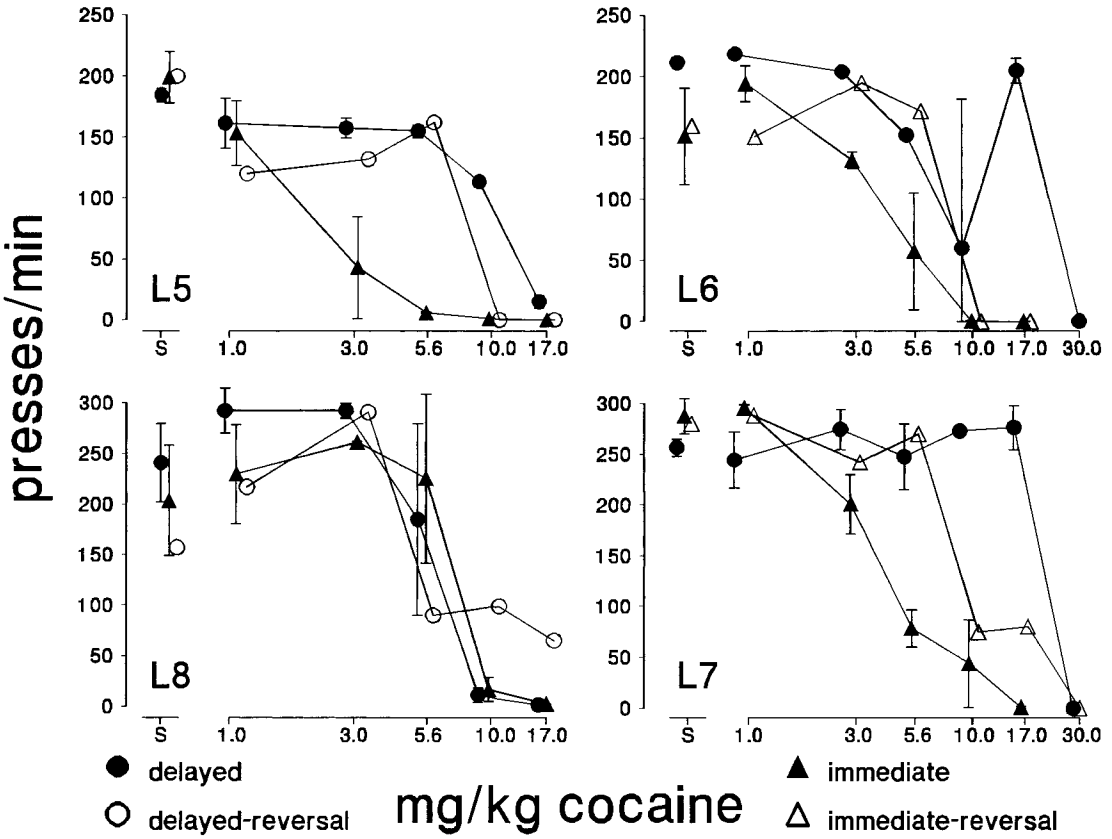

Fig. 2. The effects of cocaine on response rates of each rat in each feeding condition. Filled circles represent data from the delayed-feeding condition, open circles represent data from reversals to the delayed-feeding condition, filled triangles represent data from the immediate-feeding condition, and open triangles represent data from reversals to the immediate-feeding condition. Error bars represent ranges when dose effects were studied twice before the feeding condition was changed.

Cocaine generally decreased overall rates of responding for all rats, with dose–response curves shifted to the left under immediate-feeding conditions for 3 of 4 rats (Figure 2). This effect was retained upon reversal to the immediate-feeding conditions for Rats L6 and L7, although the curves were shifted slightly to the right of those obtained during the initial exposure to this condition. In the immediate-feeding condition for Rats L6 and L7, large decreases in rates occurred when 5.6 mg/kg (initial immediate condition) or 10.0 mg/kg (reversal condition) were administered. Their rates were not consistently suppressed in the delayed-feeding condition until 30.0 mg/kg was administered. (Response rates of Rat L6 following administration of 10.0 mg/kg cocaine during the delayed-feeding condition were not affected once, but were completely suppressed twice, despite the fact that 17.0 mg/kg did not suppress rates on either of the tests of this dose. We were unable to detect a technical reason for this unusual effect, such as an apparatus failure or unusual handling of the subject.) Under delayed-feeding conditions, Rat L5's rates were not suppressed until 17.0 mg/kg (initial delayed condition) or 10.0 mg/kg (reversal condition) was administered, whereas 3.0 to 5.6 mg/kg was sufficient to suppress responding in the immediate-feeding condition. Response rates of Rat L8 were suppressed by 10.0 mg/kg cocaine in both the initial delayed-feeding condition and in the immediate-feeding condition. In the reversal condition, large rate decreases occurred when 5.6 mg/kg was administered, but, in contrast to the previous conditions, the highest doses did

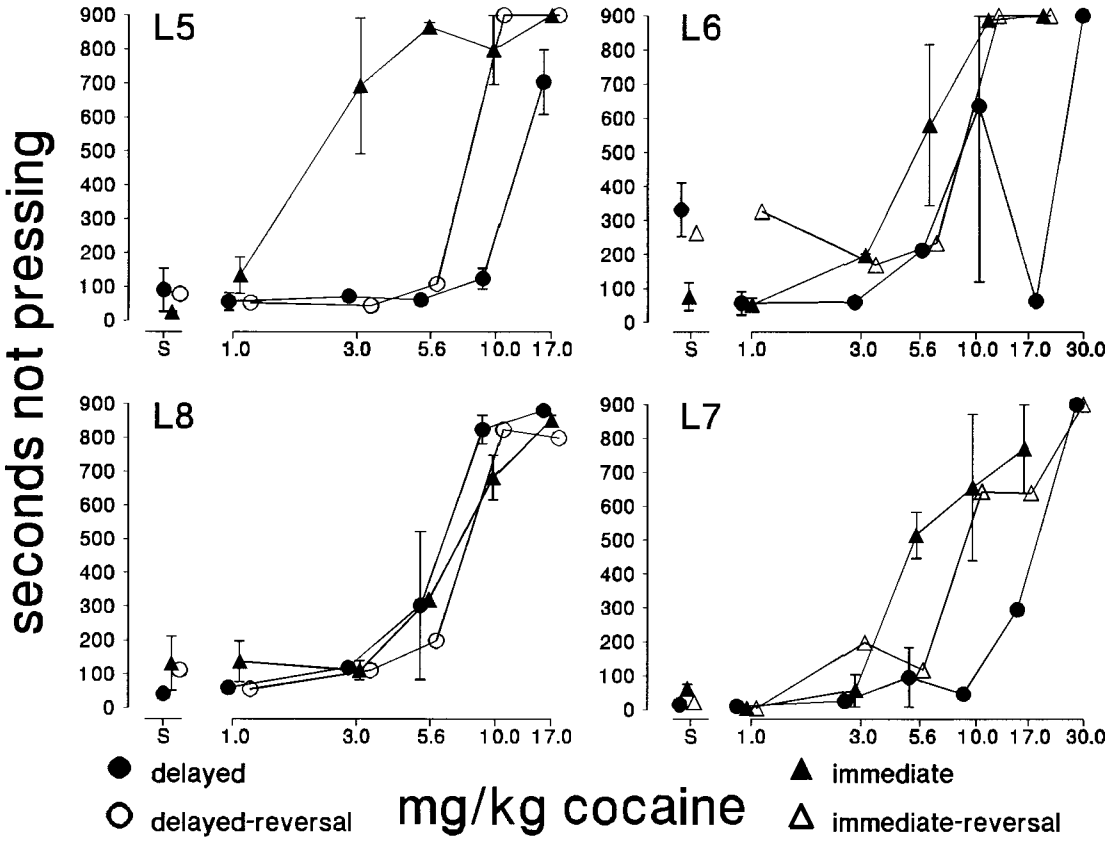

Fig. 3. Time spent not pressing for each rat as a function of cocaine under all feeding conditions. Filled circles represent data from the delayed-feeding condition, open circles represent data from reversals to the delayed-feeding condition, filled triangles represent data from the immediate-feeding condition, and open triangles represent data from reversals to the immediate-feeding condition. Error bars represent ranges.

not completely suppress rates. The order in which drug doses were administered (ascending or descending) did not systematically alter the effects of cocaine, although the order in which rats were exposed to the different feeding conditions may have altered the sensitivity of the rats to high doses of cocaine (cf. rate-suppressive doses of Rats L5 and L8 to those of Rats L6 and L7). In summary, overall rates of responding decreased as a function of dose, with decreases occurring at higher doses of cocaine in the delayed-feeding condition in 3 of 4 rats and in all rats under reversal conditions.

A more detailed analysis showed how cocaine reduced overall response rates. Examination of cumulative records (not shown) revealed that postreinforcement pauses were not systematically altered by cocaine, and response-rate reductions were not confined to any particular portion of the sessions. Cocaine did increase the time rats spent not pressing the lever, however. This was shown by examining the time of each response and reinforcer to determine whether and how often interresponse times or postreinforcement pauses (referred to together with the single term *pause*) longer than 5 s occurred. If a pause of 5 s or greater occurred, that time was considered time spent not pressing, and was accumulated in a counter. If cocaine generally reduced response rates by introducing long pauses into the session, then the time spent not pressing should increase toward 900 s (the total session time) in a manner that parallels the reductions in overall response rates depicted in Figure 2. These changes are depicted in Figure 3. The effects mirror the effects of cocaine on overall rates; dose-dependent increases in time spent not

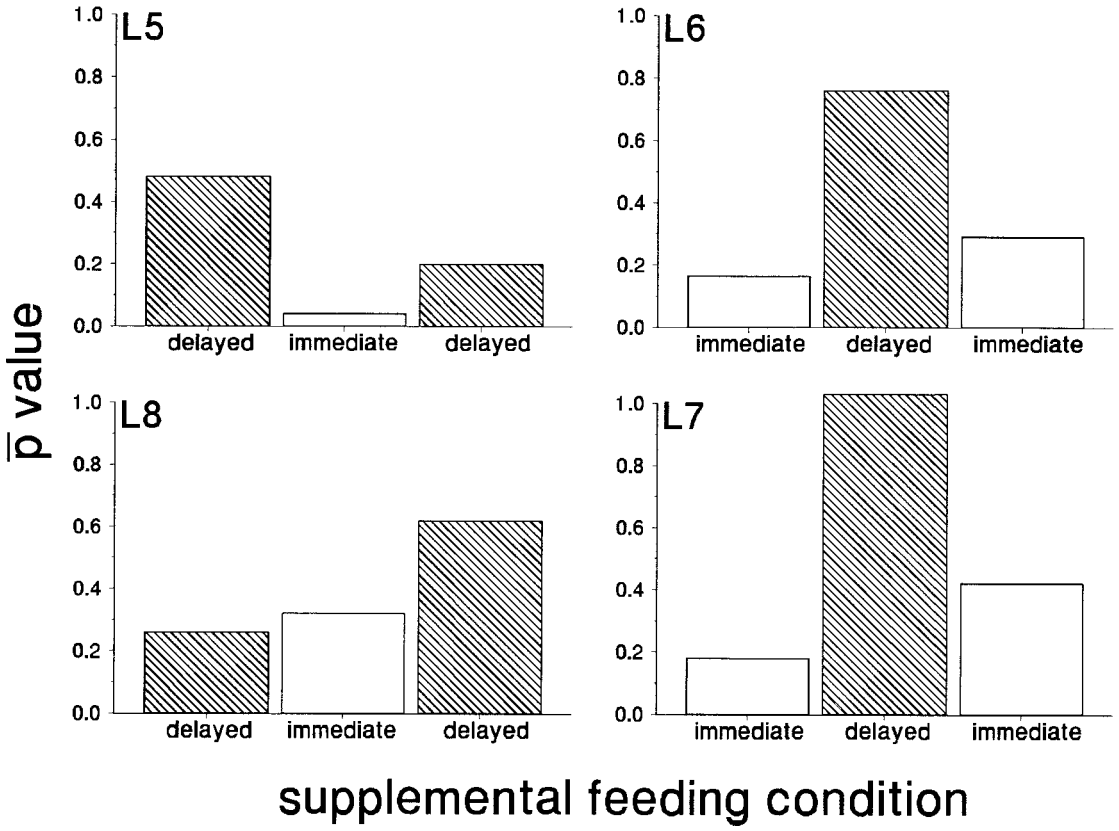

Fig. 4. Weighted means of response rates expressed as a proportion of baseline rates (i.e., $\bar{p}$ value). Open bars represent data from immediate-feeding conditions, and hatched bars represent data from delayed-feeding conditions. Bars are arranged from left to right on the *x* axis in the order in which the supplemental feeding conditions were experienced.

pressing were generally correlated with decreases in response rates.

Weighted means of response rates expressed as a proportion of baseline rates (i.e., $\bar{p}$) are shown in Figure 4. The statistic $\bar{p}$ was computed using the mean effects obtained at each dose except 30.0 mg/kg, because this dose was not administered under each condition. For 3 of 4 rats, $\bar{p}$ was higher under delayed-feeding conditions than under immediate-feeding conditions, indicating that response rates during the delayed-feeding conditions were more resistant to suppression by cocaine than rates during the reversal to the delayed-feeding condition. For Rat L8, $\bar{p}$ was highest during the reversal to the delayed-feeding condition, which reflects the fact that 10.0 and 17.0 mg/kg cocaine did not completely suppress rates.

DISCUSSION

Immediate supplemental feeding resulted in lower response rates near the ends of sessions for 2 of 4 rats (L5 and L6) relative to conditions in which supplemental feeding was delayed for 2 hr, and in those rats the lower rates were not obtained during each session (i.e., rats responded at a constant rate throughout some sessions). Lower response rates near in time to supplemental feeding have been observed in some studies (Bacotti, 1976; Collier et al., 1992; Elsmore, 1979; Hursh, 1978; Lucas et al., 1988; Timberlake, 1984; Timberlake et al., 1987; Timberlake & Peden, 1987), but in other studies lower rates near the ends of sessions have been observed regardless of the supplemental feeding conditions (McSweeney et al., 1990). Despite the fact that baseline response rates were not al-

ways lower when feeding occurred immediately after sessions, response rates were decreased by lower doses of cocaine in 3 of 4 rats when they were fed immediately following sessions compared to when they were fed 2 hr after sessions (and in each rat during the reversal conditions). Cocaine decreased overall response rates by increasing the time the rats spent not lever pressing. The cumulative proportional rate-suppressive effects of cocaine, summarized using the *p* statistic, were greater under immediate-feeding conditions than under delayed-feeding conditions.

Cocaine produced decreases in overall response rates by increasing the time spent not pressing (Figure 3). Although effects such as these have not been reported in this fashion before, they have been obtained. For example, Woolverton et al. (1978a) found that increasing doses of cocaine in rats responding under an FR 40 schedule of food reinforcement resulted in larger pauses at the beginning of sessions, followed by abrupt transitions to high-rate responding, an effect largely consistent with the effects on pausing obtained in the current study. Similar effects were obtained in pigeons by Hoffman et al. (1987). In that study, pauses encompassed entire components of a multiple schedule. Postreinforcement pauses were not uniformly increased, but large gaps in responding accounted for the rate-suppressive effects of cocaine.

Delaying supplemental feeding by 2 hr attenuated the rate-suppressive effects of cocaine in these rats. Several studies have shown that the effects of cocaine can be modified in a similar fashion by variables both within and outside the experimental situation. These include deprivation levels (Schaal & Branch, 1992; Schaal et al., 1995) and ratio values (Hoffman et al., 1987). The parallel effects of these different behavioral variables may depend on similar behavioral processes. Their commonality may be the alteration of the baseline strength of operant behavior. A characterization of response strength that has the potential to account for the behavioral effects of some drugs under some conditions may be Nevin's (1974) concept of behavioral momentum (Nevin, Mandell, & Atak, 1983). According to this notion, rate of responding is analogous to the velocity of a moving object, and the tendency for responding to continue when a disruptive force is imposed indexes a behavior's momentum or strength. Although differences in response strength in studies of behavioral momentum are typically due to differences in reinforcement rates (i.e., higher rates produce greater strength), other variables influence strength. In the present study, feeding rats immediately after sessions were completed may have decreased the reinforcing value of food during sessions, thus decreasing response strength. Cocaine, in this context conceived of as a disruptive variable, was more likely to suppress this weaker performance. This explanation of the differential effects of cocaine under the different feeding conditions in this study would be supported by data showing that the effects of more common disrupters (e.g., extinction or prefeeding) were also dependent on the time to supplemental feeding. We think that the current experiment, combined with other data on the effects of future food on current responding (Bacotti, 1976; Timberlake, 1984; Timberlake et al., 1987; Timberlake, Gawley, & Lucas, 1988), suggest strongly that the strength of food-reinforced behavior depends on the conditions of access to food outside the sessions. As such, it may be valuable to consider further the utility of response strength in research in behavioral pharmacology.

Researchers have reached different conclusions regarding the utility of a resistance-to-change analysis of the behavioral effects of drugs. Cohen (1986), for example, studied the effects of *d*-amphetamine, pentobarbital, haloperidol, and cholecystokinin on the lever pressing of rats on chained random-interval (RI) 30-s RI 30-s schedules, multiple FI 30-s FI 120-s schedules, and multiple RI 30-s RI 120-s schedules. If drug effects depend on response strength, greater disruption of response rates would be expected to occur in the initial link of the chained schedules and in the components of the multiple schedules that arranged the lower reinforcement rates (Nevin et al., 1983). Instead, behavior in the different links of the chained schedule was not differentially affected by haloperidol or pentobarbital, and *d*-amphetamine resulted in larger rate decreases (relative to baseline rates) in the terminal link than in the initial link. Under the multiple schedules, there were either no differences in rates or rates

were reduced more relative to baseline in the components with higher reinforcement rates. Cohen concluded that response-strength theory was not amenable to the interpretation of the behavioral effects of drugs.

In another study, however, the effects of methadone and buprenorphine on pigeons' rates of pecking maintained by a multiple schedule consisting of VI schedules with five different values were examined (Egli et al., 1992). Response rates maintained by schedules with lower reinforcement rates (i.e., VI 75 s and VI 150 s) were reduced at lower doses than those maintained by richer schedules (i.e., VI 10 s), consistent with Nevin's (1974) theory of response strength. In general, *p* decreased as the VI value increased, indicating that pecking maintained by leaner schedules was less resistant to disruption than pecking maintained by richer schedules. These data, in addition to the current data and those of Schaal and Branch (1992) and Hoffman et al. (1987), suggest that further investigation is warranted into conditions under which response-strength analyses will help in the understanding of the effects of drugs on operant behavior.

Cocaine, then, may fall into a more general class of disrupters (e.g., alternative reinforcement, prefeeding, extinction) that reduce operant behavior in a manner that depends on response strength. The rate-suppressive effects of cocaine may be altered by any variable (e.g., reinforcement rate, level of deprivation, etc.) that alters response strength, and the present data suggest that the time to supplemental feeding may be one of those variables. Of course, there are important differences in the precise mechanisms by which distinct behavioral variables alter response strength and in the precise mechanisms by which drugs alter behavior. Drugs are likely to interact with some strength-altering variables in ways consistent with Nevin's (1974) account (e.g., level of food deprivation; Schaal & Branch, 1992), but not with other variables (e.g., reinforcer immediacy; Cohen, 1986). We also recognize that rate suppression is but one potential effect of drugs, and that other effects (e.g., rate increases, alterations in response patterns, motoric disruption, changes in the effects of stimuli, etc.) may or may not bear any relation to response strength. We believe, however, that there are enough consistent results to justify further research designed to identify drugs and behavioral conditions that interact in this manner.

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